

ACRIDOIDEA OF THE GALAPAGOS ISLANDS  
(ORTHOPTERA)



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# ACRIDOIDEA OF THE GALAPAGOS ISLANDS (ORTHOPTERA)

By V. M. DIRSH

## SYNOPSIS

The Acridoidea of Galapagos Islands are revised. The valid species are redescribed and lectotypes are selected. The systematic position of the species is reviewed.

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## INTRODUCTION

SINCE Darwin's travels the Galapagos Islands have deservedly become famous as a sanctuary for numerous endemic species of various classes of the animal kingdom. Of them all, insects have been the least studied. However, lately this gap has begun to be filled (Linsley and Usinger, 1966).

This paper is an attempt to review the Acridoidea fauna of these islands on the basis of much material which was not available to earlier authors. The views of earlier authors are reviewed in the light of the latest taxonomic studies, which have sometimes demanded redescrptions of the types and revaluation of the taxonomic status of some of the species and subspecies. All the genera and species known from these islands are mentioned; they comprise 4 genera and 9 species.

## ACKNOWLEDGEMENTS

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## NAMES OF THE ISLANDS

Because most of the islands of the Galapagos Archipelago have more than one name (English and Spanish) and sometimes two different islands (Gardner Is.) have the same name, a list showing the names and synonyms is given below. In this paper the English names are used.

<i>English names</i>	<i>Spanish names</i>
Abingdon	Pinta, Geraldino
Albermarle	Isabela, Santa Gertrudis
Barrington	Santa Fé
Bartholomew	Bartholomé
Bindloe	Marchena, Torres
Champion	—
Charles	Santa Maria, Floreana
Chatham, Dassigney	San Cristóbal, Grande
Culpepper	Darwin, Guerra
Daphne Major	—
Daphne Minor	—
Duncan, Dean	Pinzón
Eden	—
Gardner-near-Charles	—
Gardner-near-Hood	—
Hood	Española
Indefatigable, Norfolk, Porter	Santa Cruz, Bolivia, Chavez, San Clemente, Valdez
James, York	San Salvador, Santiago, Gil, Olmedo
Jervis	Rábida
Narborough	Fernandina, Plata
North Seymour	Seymour
—	Plaza
South Seymour	Baltra
Tower, Ewres	Genovesa
Wenman	Wolf, Gasna, Nunez

## ZOOGEOGRAPHICAL REMARKS

The finches observed by Darwin on the Galapagos Islands attracted the attention of the whole scientific world. Their specialization was attributed to the insular isolation. Van Denburgh (1914) and many other authors noticed that land tortoises and iguanas from different islands, although of the same species, could be distinguished and their origin in each case from a particular island or even part of an island could be determined. The differences within species are probably due not only to physical isolation but also the 'territorial instinct' of these animals. They are attached to their breeding places and there is evidence (Eibl-Eibesfeldt, 1960) that every individual claims its own bit of territory and even fights for it, protecting its

rights. This same territorial instinct has been observed also in crabs. In Acridoidea, species of the genus *Schistocerca* are good fliers and can easily cover the distances between the islands, and the territorial instinct has never been observed in Acridoidea.

Snodgrass (1902) erected several subspecies of *Schistocerca melanocera* (Stål, 1861), and Scudder (1893) several subspecies of *Schistocerca literosa* (Walker, 1870), but both authors based their subspecies on insufficient material and considered the range of variability of the species as racial; when more material from various island was available it became clear that the 'subspecies' fit into the range of variability of the species from a single island. Hebard (1920) and the present author synonymized these subspecies and one species.

A different picture arose when the genus *Halmenus* was studied. The species of this genus are brachypterous or micropterous and cannot fly. All of them are morphologically very similar, but the populations from different islands can be distinguished. It is clear that the various forms of *Halmenus* could appear only as a result of physical isolation, and since the males' internal genital organs are very similar, the isolation has probably not been of long duration.

In the case of the genus *Sphingonotus* the position is rather similar to *Schistocerca*. All the species are macropterous and can fly. However, the species of *Sphingonotus* are small and according to observation they are not long-distance fliers but can be carried by the wind. In the Galapagos Islands much more variability can be observed in *Sphingonotus* than in *Schistocerca*, and possibly there is already a tendency to form races on the different islands.

Concerning the genera *Closteridia* (*C. bauri* Scudder, 1893) and *Desmopleura* (*D. concinna* Scudder, 1893), the former is known by the type only and the latter by only a few specimens.

How did Acridoidea populate the Galapagos Archipelago? The islands may have been nearer to the continent, or they may even have been connected with it and have separated by Continental Drift (Cox, 1966). However, in a later paper it was suggested that they are of rather recent origin. Cox and Dalrymple (1966), on the basis of palaeomagnetism and Potassium-Argon measurements, determined that the rocks exposed above sea level were extruded during the Brunhas Matuyama polarity epochs and this process took place only about 2.4 million years ago. In any case the islands could be populated from the continent only, the shortest distance of which now is about 500 miles. Some species, such as *Schistocerca melanocera* and *literosa*, could easily fly such distances, particularly if winds were favourable. The small, winged species of *Sphingonotus* could travel the same way. Wingless and short-winged species could be carried to the Archipelago by the oceanic currents, with debris.

Orr (1966) observed that vegetation debris was carried by the rivers of South America down to the coast and into the sea, where they formed raft-like masses up to 10 ft. in diameter. There they were caught by the South Equatorial Current and Humboldt Current and, according to Orr's calculation, could theoretically reach the Galapagos Islands in less than two weeks.

If we accept the estimate of Cox and Dalrymple (1966) concerning the time of origin of the Galapagos Islands, then the evolutionary changes in the Galapagos

Acridoidea took a remarkably short time. There is on the continent no species of *Schistocerca* very closely related to the Galapagos species. The same applies to the three genera *Desmopleura*, *Closteridia* and *Halmenus* and partly to *Sphingonotus*. The species of the latter have a very near relative on the Puna Islands, which are only about two miles from the Ecuador shore.

### *SCHISTOCERCA* Stål, 1873

*Acridium* (*Schistocerca*) Stål, 1873.

*Schistocerca* Stål, 1876.

The genus *Schistocerca* belongs to the subfamily Cyrtacanthacridinae of Acrididae. It contains numerous species on the American continent and one in the Old World (Africa and South-west Asia), but occasional specimens sometimes fly, aided by air currents, far from the usual area of distribution.

In the Galapagos Archipelago, according to the studies presented in this paper, there are only two species of this genus. How they populated these islands we can only guess. It could have been by free flight or by being carried by the wind or oceanic currents. They certainly came from the American continent, and probably from the northern part of South America. Apparently there are in America no species closely related to the two Galapagos species. However, it must be noted that the genus *Schistocerca* is probably of comparatively recent origin and is expanding, forming numerous forms and variations. An indication of this possibility is that the internal genitalia are very similar in all the species of the genus, in America, the Old World and the Galapagos Islands. The variability within the species, particularly the American ones, is very great. The external morphological characters are as similar between species as the phallic complex and in many cases only morphometric characters, pattern and coloration serve to distinguish the species.

There are not in America or in the Old World any genera which can be considered to be closely related to *Schistocerca*; the main characters—the flattened plate-like cerci in combination with the excised distal end of the subgenital plate in males—do not occur in such a combination in other genera of the subfamily.

However, in the genus *Halmenus*, which occurs only in the Galapagos Islands, there is a small excision on the male subgenital plate, though smaller than in *Schistocerca*, and the cerci are flattened as well, but of angular shape, unlike those of *Schistocerca*. The internal genitalia are so similar to those of *Schistocerca* that they can be easily confused, and the spermatheca is also extremely similar. The mesosternal lobes of *Halmenus* are not fully typical of Cyrtacanthacridinae, but are not sufficiently atypical to exclude the genus from this subfamily.

There is thus much scope for speculation concerning the origin of *Schistocerca* and its relationship with other genera, but the author feels that the time is not at present ripe for it. The American genera *Abracris* and *Osmilia* (both long-winged) occupy the same indefinite position as *Halmenus* and they too should perhaps be placed into Cyrtacanthacridinae. This would complicate the question of the relationship of *Schistocerca* even more, particularly because hitherto it has been regarded

as the only representative of the subfamily Cyrtacanthacridinae in the whole of America.

It is obvious that further study of the South and Central American fauna is urgently needed before definite conclusions can be reached.

The distribution of the two species of the genus on the Galapagos Islands is rather peculiar. On the information at present available it can be stated (but not yet explained because of lack of information) that *S. melanocera* inhabits almost all the islands of the Archipelago, while *S. literosa* occurs only on islands on the south-eastern fringe of it (see map).

*Schistocerca melanocera* (Stål, 1860)

(Pl. 1, Text-figs. 1-12, Map 1)

*Acridium melanocerum* Stål, 1860 : 326. Type ♀. 'Insulae Galapagos'. Naturhistoriska Rikmuseet, Stockholm.

*Acridium tibiale* Walker, 1870 : 582 (Kirby, 1910 : 457). Type ♂. 'West coast of America'. British Museum (Natural History), London.

*Acridium (Schistocerca) melanocerum* Stål, 1860 : 326 (Stål, 1873 : 65).

*Schistocerca melanocera* (Stål, 1860) (Bruner, 1889 : 193).

*Schistocerca melanocera minor* Snodgrass, 1902 : 421 (Hebard, 1920 : 323). LECTOTYPE ♀. 'Tagus Cove, Albemarle'. By present selection from 6 ♂ and 6 ♀ syntypes. Los Angeles County Museum of Natural History, U.S.A.

*Schistocerca melanocera pallida* Snodgrass, 1902 : 422 (Hebard, 1920 : 323). LECTOTYPE ♀. 'Barrington Is.' By present selection from 5 ♂ and 2 ♀ syntypes. Los Angeles County Museum of Natural History, U.S.A.

*Schistocerca melanocera lineata* Snodgrass, 1902 : 423 (Hebard, 1920 : 323). LECTOTYPE ♀. 'Albemarle Is. Iguana Cove.' By present selection from 7 ♂ and 8 ♀ syntypes. Los Angeles County Museum of Natural History, U.S.A.

*Schistocerca melanocera immaculata* Snodgrass, 1902 : 423 (Hebard, 1920 : 323). LECTOTYPE ♂. 'Indefatigable Is.' By present selection from 3 ♂ and 3 ♀ syntypes. Los Angeles County Museum of Natural History, U.S.A.

*Schistocerca intermedia* Snodgrass, 1902 : 431. **Syn. n.** Type ♀ (lost). 'Duncan Island.' *Neotype* ♀. 'Pinzon Island.' = Duncan Is. California Academy of Sciences, U.S.A.

*Schistocerca intermedia borealis* Snodgrass, 1902 : 435. **Syn. n.** LECTOTYPE ♂ by present selection from 2 ♂ and 1 ♀ syntypes, Bindloe Is. Los Angeles County Museum of Natural History, U.S.A.

All subspecies of *Schistocerca melanocera* were rightly synonymized by Hebard, 1920. They cannot be separated either by morphological, colour or morphometric characters. Using a few specimens from the different islands, the difference, even if it is very small, can sometimes be detected, but as soon as a series is available the material becomes a continuous series, which cannot be separated according to the islands' sources. For example, the subspecies *melanocera melanocera* (*sensu* Snodgrass) from Charles Island possesses a yellowish spot on the lateral lobe of the pronotum. On the basis of this spot, Snodgrass (1902) considered it to be a subspecies. On Charles Island most specimens possess this spot, but some do not. On the other hand some specimens from Barrington, Albemarle, North and South Seymour, James, Narborough, Jervis, Darwin and some other islands also possess it. This invalidates the character as a subspecific one.

It is well known that coloration and partly pattern depend very much not only on the genotypical basis of the population but also on the colour of the environment in which the specimens grow and live.

The same considerations are applicable to the other characters used by Snodgrass for differentiation of the subspecies. They are even weaker in this respect than the yellowish spot on the pronotum.

The newly synonymized *Sch. intermedia* belongs to the same category. The type of it is lost, but the topotypical material from Duncan Is., which agrees with Snodgrass' description, differs from the typical *melanocera* only in the paler greyish general coloration and in the more pronounced spots on the tegmina. No morphological or morphometric differences were found. This coloration is probably the result of the specimens having developed on a lighter-coloured background. To attribute to them specific or even subspecific value is not possible for the above reasons and also because some of the specimens from Barrington, Chatham and Jarvis Islands are practically identical with the *intermedia* from Duncan Island.

The subspecies *Sch. intermedia borealis* is characterized only by the more developed pattern of the tegmina; in all other respects it is the same as *melanocera* and *intermedia*.

The opinion was expressed (Hebard, 1920) that *Sch. intermedia intermedia* is an intermediate form between *Sch. melanocera* and *literosa*. But a morphometric study showed that they can be differentiated, the hind femur being relatively longer and narrower in *melanocera* than in *literosa*.

The variability in the size of the body of *Sch. melanocera* is rather great, but it cannot be associated with any particular island.

Redescription. ♂. Large. Integument slightly rugose and pitted. Antenna longer than head and pronotum together. Fastigium of vertex short, obtuse-angular, with shallow oval depression in middle; frontal ridge low, with margins parallel and slight depression at ocellus. Dorsum of pronotum subcylindrical, slightly widening backwards and slightly constricted in anterior half; median carina low, linear, crossed by three deep sulci; metazona slightly longer than prozona, its posterior margin obtuse-angular to almost rounded; lateral lobes in prozona concave. Prosternal process from narrow cylindrical to subconical, at apex rounded. Mesosternal interspace about twice as long as its width in middle, slightly widening in front. Tegmina and wings far exceeding end of abdomen. Opening of tympanal organ almost semi-circular, membrane deeply set forming wide angle with body wall. Hind femur comparatively long and narrow, average ratio of length to maximum width 4.87. Hind tibia as long as femur. Supra-anal plate elongate-angular, in middle of basal part with longitudinal sulcus merging with lateral carinulae, sides upcurved, forming ridge-like elevations. Cercus slightly narrowing towards apical part; upper half of apex angularly protruding. Subgenital plate in profile short, narrow, at apex attenuate.

Phallic complex: of usual structure for the genus; apical valves of penis shorter than valves of cingulum.

Coloration: in general, from shiny dark brown to dull brownish grey. Antenna blackish; face as general coloration, with longitudinal yellowish or ochraceous stripes on sides of frontal ridge and on genae; prozona of pronotum blackish or brown; metazona from yellowish to dull ochraceous; in upper part of lateral lobe of prozona sometimes a small yellowish spot; head above, with yellowish narrow stripe, which merges with yellowish median carina; tegmen uniformly shiny blackish or brown, sometimes with a few dark brown spots in medial area, sometimes dull brownish or greyish with spots more developed and scattered over whole tegmen; membrane in dark specimens less transparent than in greyish ones; wing blackish or infumate; outer side of hind femur blackish with yellowish longitudinal stripe in lower part of medial area, upperside

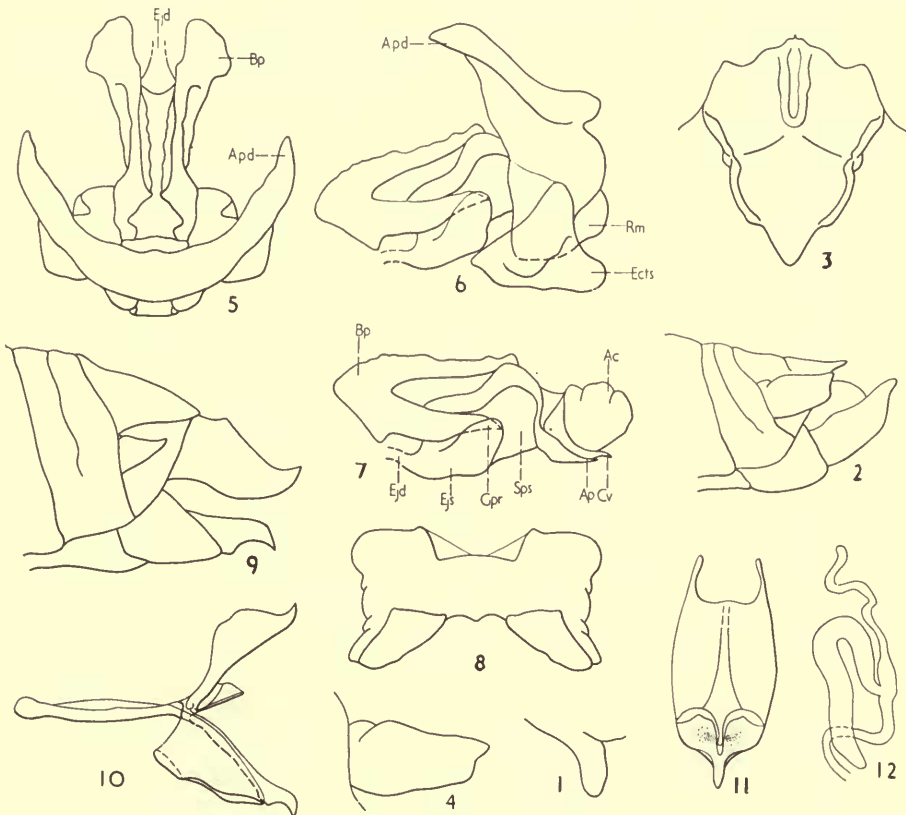


with two indefinite, brown, transverse fasciae, in greyish specimens the blackish upper part of medial area greyish and sometimes tending to disappear; hind tibia yellow.

♀. Larger than male. Ovipositor, in profile, comparatively short and wide; upper valve about half as wide as long. In other respects as male.

### Measurements

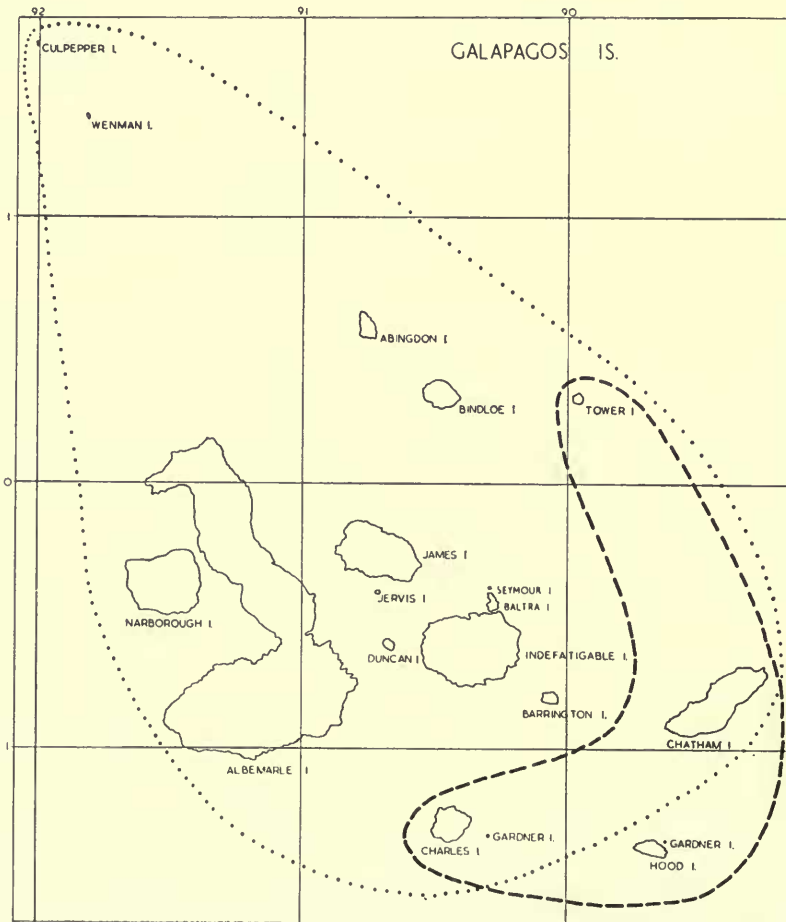
		Length of body	Length of pronotum	Length of tegmen	Length of hind femur	Ratio of length to width, of hind femur
♂	Range	30.7-49.1	6.2-8.2	32.1-49.0	17.4-25.5	4.4-5.4
	Average	40.2	7.7	41.7	21.1	4.87
♀	Range	41.4-64.5	7.7-12.3	44.9-65.5	21.5-32.3	4.5-5.9
	Average	54.3	10.4	55.5	27.8	5.02



FIGS. 1-12. *Schistocerca melanocera*. 1-8, ♂: 1, prosternal process; 2, end of abdomen, side view; 3, supra-anal plate; 4, left cercus; 5, phallic complex from above (epiphallus and most of ectophallic membrane removed); 6, the same, lateral view; 7, endophallus, lateral view; 8, epiphallus (bridge in horizontal position). 9-12, ♀: 9, end of abdomen lateral view; 10, sclerotized parts of ovipositor; 11, subgenital plate, inner view; 12, spermatheca.

Geographical distribution: Abingdon, Albemarle, South Seymour, Barrington, Charles, Chatham, Culpepper, Duncan, Gardner (near Charles), Indefatigable, James, Jervis, Narborough, Tower.

The main differences between *Sch. melanocera* and *Sch. litorosa* are in size and coloration. Their phallic complexes are rather similar. Measurements overlap, but there is one morphometric character by which it is possible to separate these two species: the hind femur is relatively more slender and narrower in *Sch. melanocera* than in *Sch. litorosa*. This difference can be detected visually, and statistically it is as follows: Ratio of length to maximum width of hind femur in *melanocera* is in males: mean 4.87, standard deviation  $\pm 0.23$ , standard error  $\pm 0.02$ ; and in females: mean 5.02, standard deviation  $\pm 0.21$ , standard error  $\pm 0.02$ . The corresponding ratio in *litorosa* is in males mean 4.47, standard deviation  $\pm 0.23$ , standard error  $\pm 0.04$ ; and in females: mean 4.55, standard deviation  $\pm 0.20$ , standard error  $\pm 0.04$ .



MAP I. Area of distribution of *S. melanocera* (dotted line) and *S. litorosa* (interrupted line).

The difference of means between these two species is: in males 0.41, standard error  $\pm 0.04$ ,  $t$  9.37,  $df$  264,  $P < 0.001$ ; and in females 0.48, standard error  $\pm 0.04$ ,  $t$  10.97,  $df$  163,  $P < 0.001$ .

This character places the synonymized *Sch. intermedia* in *Sch. melanocera*.

*Schistocerca literosa* (Walker, 1870)

(Pl. 2, Map 1, Graph 1; Text-figs. 13-24)

*Acridium literosum* Walker, 1870 : 620. Type ♂. 'Galapagos Is.' British Museum (Natural History), London.

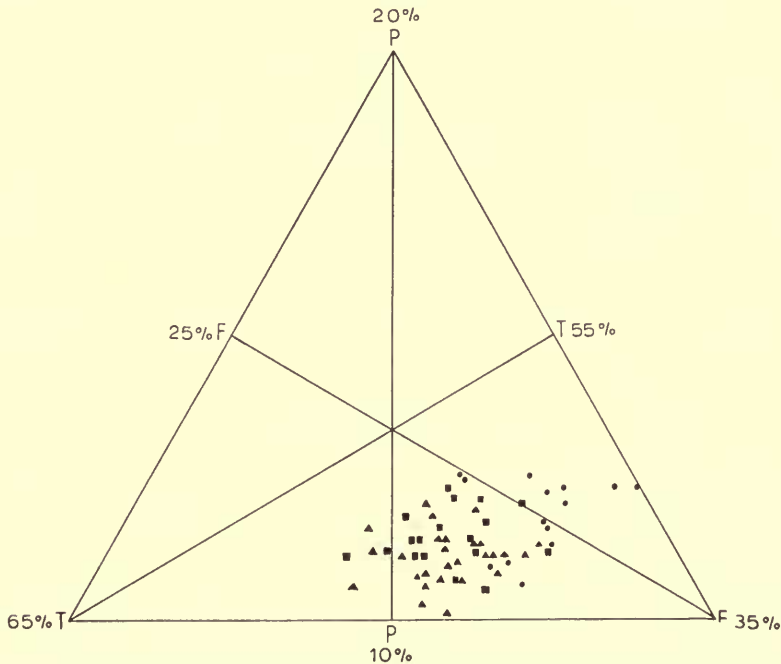
*Schistocerca literosa* (Walker, 1870) (Scudder, 1893 : 15)

*Schistocerca literosa discoidalis* Scudder, 1893 : 16 (Hebard, 1920 : 425). LECTOTYPE ♂. 'Chatham Is., Wreck Bay.' By present selection. Museum of Comparative Zoology, Harvard University, U.S.A. Syntype ♀. Locality and Museum as for Lectotype.

*Schistocerca literosa punctata* Scudder, 1893 : 16. **Syn. n.** Syntype ♀. 'Hood Is.' Museum of Comparative Zoology, Harvard University.

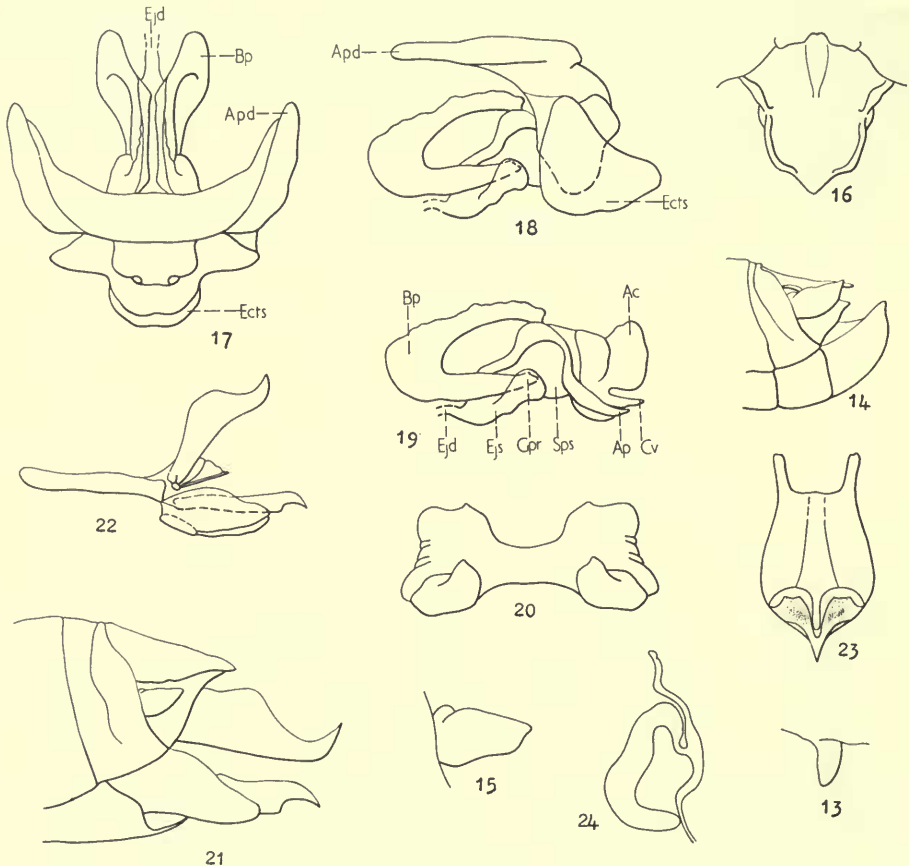
*Schistocerca literosa hyalina* Scudder, 1893 : 16. **Syn. n.** Syntype ♂. 'Tower Is.' Museum of Comparative Zoology, Harvard University.

*S. literosa* can be separated morphometrically (see above) from *Sch. melanocera* by the relatively shorter and wider hind femora.



GRAPH 1. Triangular co-ordinates showing distribution of proportional values of length of pronotum (P), length of tegmen (T), and length of hind femur (F), expressed as percentages. ●—Chatham Is., ▲—Hood Is., ■—Tower Is. of *S. literosa*.

The three subspecies of *literosa* described by Scudder were attributed by him to three different islands. The differences of characters were tabulated by him, but when the types and topotypical material were studied, it was clear that not a single character or any combination could be used to separate the subspecies. These three forms overlap widely and are present in the population of every island. The populations from Hood and Tower Islands merge completely in every respect, including size (Graph I). The Chatham population overlaps widely but not completely with the populations of Hood and Tower, the tegmina of Chatham specimens being relatively longer (Graph 1), but not so much that it would be advisable to consider them as a separate race. Probably interchange between these islands occurs regularly, so that their populations become almost homogeneously mixed.



FIGS. 13-24. *Schistocerca literosa*. Type. 13-20, ♂: 13, prosternal process; 14, end of abdomen, lateral view; 15, left cercus; 16, supra-anal plate; 17, phallic complex from above (epiphallus and most of ectophallic membrane removed); 18, the same, lateral view; 19, endophallus, lateral view; 20, epiphallus (bridge in horizontal position, whole epiphallus slightly shrunk). 21-24, ♀: 21, end of abdomen, lateral view; 22, sclerotized parts of ovipositor; 23, subgenital plate, inner view; 24, spermatheca.

Redescription. ♂. Of medium size. Integument slightly rugose and pitted. Antenna longer than head and pronotum together. Fastigium of vertex short, obtuse-angular, in middle with rhomboidal depression; frontal ridge low, with margins parallel and slight depression at ocellus. Dorsum of pronotum flattened, slightly constricted in prozona and widened in metazona; metazona slightly longer than prozona, its posterior margin rounded; median carina thin, linear, crossed by three sulci; lateral lobes of prozona concave in middle. Prosternal process from narrow, conical, at apex obtuse, to almost cylindrical. Mesosternal interspace twice as long as its width in middle, slightly constricted and widened in front. Tegmina and wings wide, exceeding end of abdomen. Opening of tympanal organ almost semi-circular, membrane deeply set, forming wide angle with body wall. Hind femur comparatively short and wide, average ratio of length to maximum width 4.47. Hind tibia slightly shorter than femur. Supra-anal plate elongate-angular, in middle of basal part with longitudinal sulcus, which sometimes extends to middle of apical half; sides upcurved and elevated. Cercus narrowing towards apical part, apex oblique, with upper angle protruding. Subgenital plate, in profile, short, moderately narrow, at apex slightly narrowed.

Phallic complex: of usual structure for the genus; apical valves of penis shorter than valves of cingulum. It differs from *melanocera* in the shape of the basal valves of the penis and in the epiphallus, the latter in *literosa* having more developed and more acute lophi.

Coloration: in general, grey or sometimes brownish. Pronotum uniformly coloured, or mottled with darkish spots, frequently on upper part of lateral lobe or prozona with a small ochraceous spot; tegmen covered with dark brownish spots, sometimes poorly defined, sometimes very sharp; membrane from greyish to transparent colorless; wing hyaline, practically colorless; hind femur above with three transverse brownish fasciae, sometimes extending to outer and partly to inner sides; hind tibia yellowish.

♀. Larger than male. Ovipositor, in profile, comparatively long and narrow; upper valve about one-third as wide as long.

### Measurements

		Length of body	Length of pronotum	Length of tegmen	Length of hind femur	Ratio of length to width of hind femur
♂	Range	27.3-34.5	5.1-6.3	26.4-35.2	13.9-18.9	4.1-4.9
	Average	31.4	6.1	30.6	16.3	4.47
♀	Range	34.6-43.4	6.7-7.7	33.7-43.8	17.7-22.6	4.0-5.0
	Average	39.9	7.5	38.4	20.1	4.55

Geographical distribution: Chatham, Hood, Gardner (near Hood), Tower, Charles, Gardner (near Charles).

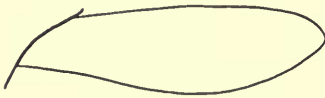
### *HALMENUS* Scudder, 1893

Four species of this genus have been described. All of them possess strongly shortened tegmina and wings and cannot fly. They could populate different islands by means of floating debris brought by currents, but there is also the possibility that they were able to fly when the islands were populated and afterwards rapidly lost this ability.

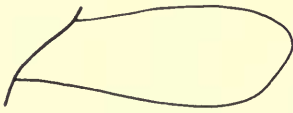
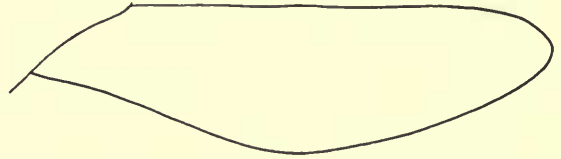
Owing to the loss of the ability to fly, the populations of the islands have been completely or almost completely isolated. As a result, the genus formed species which can be differentiated by external morphological characters and partly by the structure of the phallic complex.

## KEY TO SPECIES

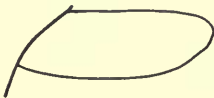
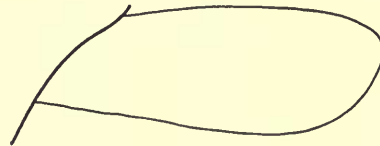
- 1 (2) Tegmina overlapping dorsad; anterior margin of tegmen strongly excurved, apex narrowed (Text-fig. 25) . . . . . **robustus** Scudd.
- 2 (1) Tegmina not overlapping dorsad; anterior margin of tegmen straight or only slightly excurved, apex rounded or slightly attenuate
- 3 (6) Male cercus narrow, angular, at apex obtuse or acute. Interocular space narrower or as wide as antennal scape. Upper outer margin of upper valve of ovipositor irregularly serrated.
- 4 (5) Male cercus narrow, at apex acute or subacute. Tegmina reaching or slightly exceeding middle of second abdominal tergite . . . . . **cuspidatus** Snodgr.
- 5 (4) Male cercus narrow, comparatively short, at apex obtuse. Tegmina slightly exceeding end of first abdominal tergite . . . . . **choristopterus** Snodgr.
- 6 (3) Male cercus wide, angular, at apex obtuse, almost rounded. Interocular space wider than antennal scape. Upper margin of upper valve of ovipositor smooth (Text-fig. 51) . . . . . **eschatus** Heb.



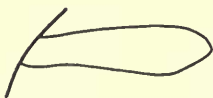
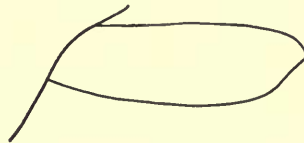
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28



FIGS. 25-28. Tegmina of *Halmenus*. Left, ♂, right, ♀. 25, *robustus*; 26, *cuspidatus*; 27, *choristopterus*; 28, *eschatus*. All drawn to the same scale.

In the structure of the phallic complex and of the spermatheca, in the shape of the lobes of the mesosternum and in the incised male subgenital plate, *Halmenus* considerably resembles *Schistocerca*. It is different from *Schistocerca* in other respects, but these similarities suggest strong affinity between the two genera and because of them *Halmenus* is here placed in the subfamily Cyrtacanthacridinae.

Type-species: *Halmenus robustus* Scudder, 1893.

*Halmenus robustus* Scudder, 1893

(Pl. 2, Text-figs. 29-39)

♂ (Type. Redescription). Integument finely rugose and pitted. Antenna filiform, shorter than head and pronotum together, 24-segmented. Fastigium of vertex longer than wide, slightly concave in middle, angular, apex obtuse; sides and apex strongly pitted; frontal ridge almost flat; lateral carinulae obliterated; facial carinulae well developed. Pronotum comparatively long, slightly constricted at sides in posterior part; dorsum subcylindrical, crossed by 3 deep sulci; median carina in prozona almost obliterated, in metazona linear, obtuse; metazona much shorter than prozona, its posterior margin obtuse-angular; lateral lobe longer than high, in prozonal part convex, at posterior sulcus concave, lower margin sinuate. Prosternal process narrow, conical. Mesosternal interspace about twice as long as wide, slightly widening towards front; mesosternal lobes long, angular, with angles obtuse. Metasternal interspace strongly elongate, narrow. Tegmina overlapping dorsad, shortened, reaching fourth abdominal tergite, venation coarse. Wings shorter than tegmina. Hind femur moderately slender, exceeding end of abdomen; lower lobes of hind knee rounded. Hind tibia at apical part slightly widened; external apical spine absent. Arolium large, longer than claw. Last abdominal tergite with a pair of large, wide projections. Supra-anal plate angular, longer than wide, apex angularly attenuate; median longitudinal carinula present, bifurcate in basal part; base with a pair of marginal, lateral projections; transverse fold well pronounced. Cercus acute-angular, compressed from sides, at apex acute. Subgenital plate obtusely conical, at apex excised.

General coloration ochraceous. Lateral lobe of pronotum, in upper part of prozona, with shiny, dark brown, wide longitudinal stripe, at lower margin of which there is a narrow yellowish stripe; post-ocular brown stripe similar to pronotal one.

♀. Larger than the male. Ovipositor slender; upper outer margin of upper valve of ovipositor roughly serrated.

Length: ♂ 20.0-23.0, ♀ 26.0-36.2; pronotum ♂ 4.8-5.7, ♀ 6.2-7.2; tegmen ♂ 5.4-6.1, ♀ 7.1-10.9; hind femur ♂ 12.0-13.4, ♀ 14.4-17.0 mm. (Measurements based on material studied by the author.)

Type ♂. Type locality: 'Conway Bay, Indefatigable Island. Galapagos'. Type No. 15335. (It must be considered as a Syntype, since Scudder's description is based on two males and one female.) Museum of Comparative Zoology, Harvard University, U.S.A.

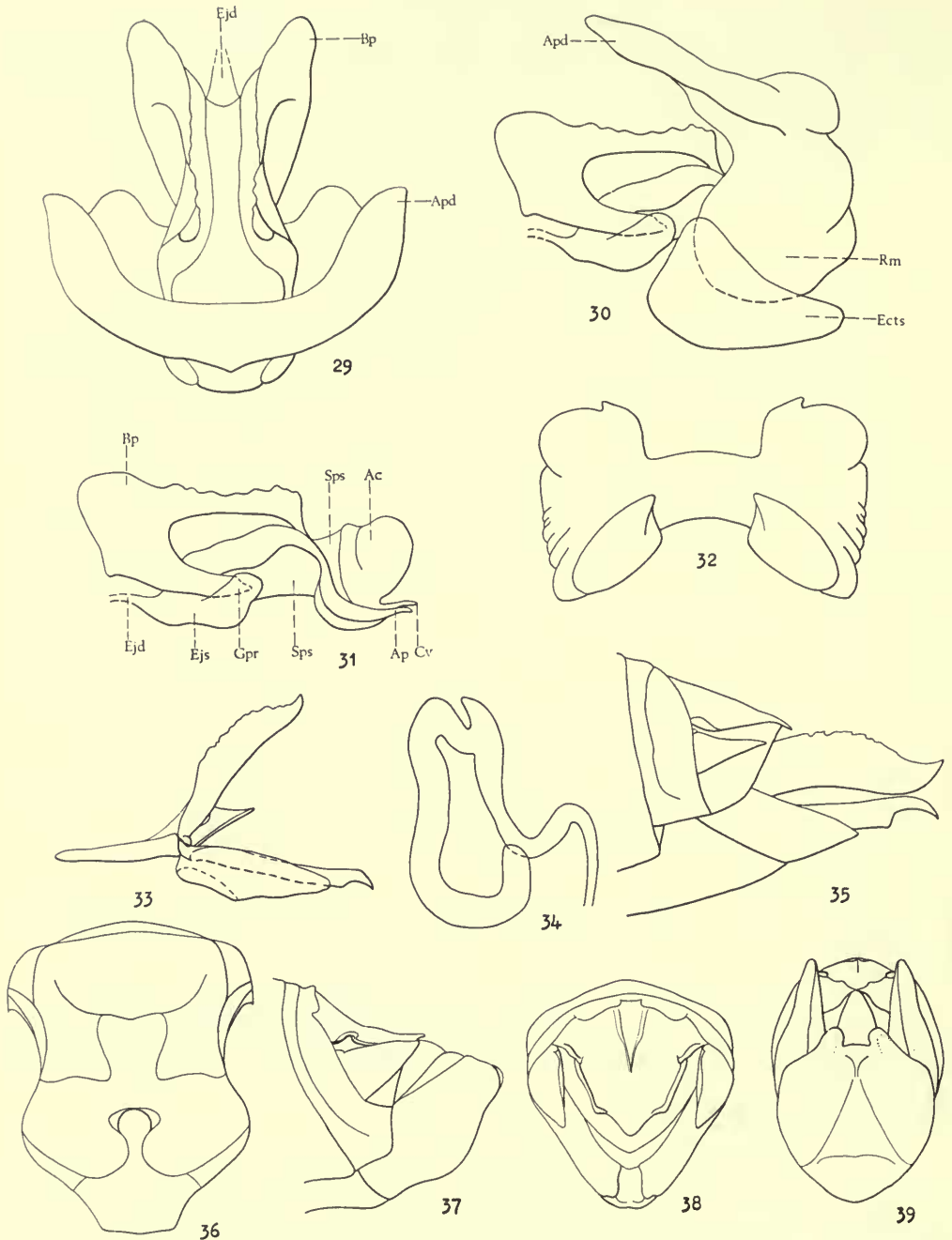
Geographical distribution: Indefatigable, James.

*Halmenus cuspidatus* Snodgrass, 1902

(Text-figs. 26, 40-43)

Differs from other species of the genus in the characters indicated in the key.

In female, upper outer margin of upper valve of ovipositor roughly serrated. Length: ♂ 19.0-22.8, ♀ 26.4-29.5; pronotum ♂ 4.8-5.0, ♀ 6.4-6.7; tegmen ♂ 4.8-



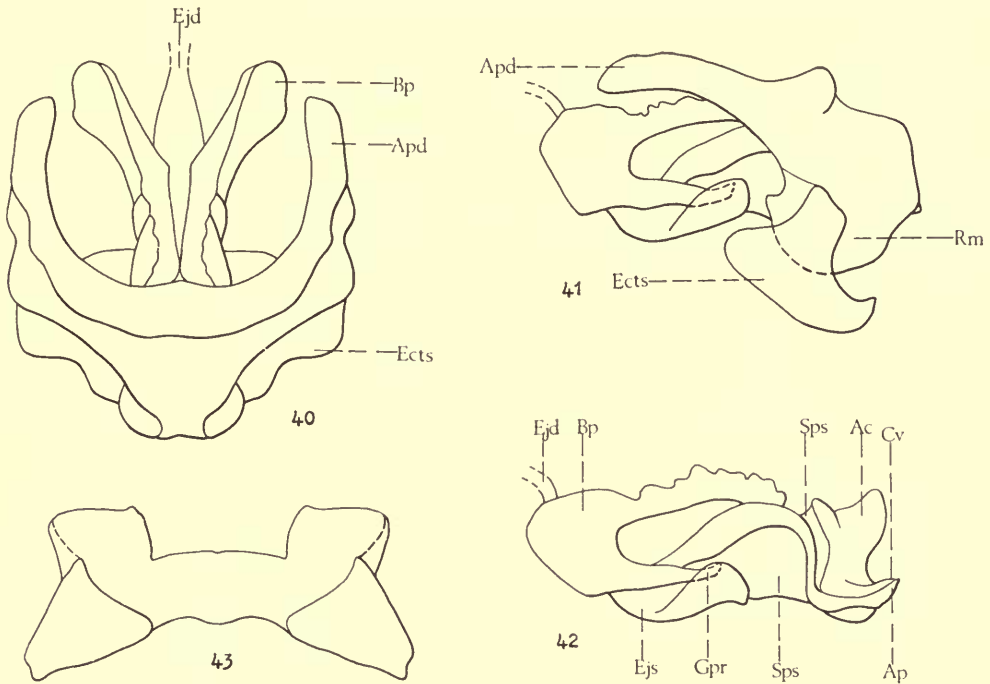
FIGS. 29-39. *Halmenus robustus*. 29, phallic complex, from above (epiphallus and most of ectophallic membrane removed); 30, the same, lateral view; 31, endophallus; 32, epiphallus. 33, sclerotized parts of ovipositor; 34, spermatheca; 35, end of abdomen; 36, meso- and metasternum; 37, end of abdomen from lateral view; 38, the same, from above; 39, the same, posterior view, to show excision on end of subgenital plate.



5.0, ♀ 5.2-6.1; hind femur ♂ 12.5-13.6, ♀ 14.8-16.0 mm. (Measurements based on material studied by the author.)

Type ♀. Type locality: Albemarle Is., Iguana Cove. Type lost.

Geographical distribution: Albemarle.



FIGS. 40-43. *Halmenus cuspidatus*. Phallic complex. 40, from above (epiphallus and most of ectophallic membrane removed); 41, the same, lateral view; 42, endophallus; 43, epiphallus.

### *Halmenus choristopterus* Snodgrass, 1902

(Text-fig. 27)

Differs from the other species of the genus in the characters indicated in the key. Tegmina in both sexes shorter than in *cuspidatus*. In female, upper outer margin of upper valve of ovipositor roughly serrated.

Length: ♂ 22.3, ♀ 25.1-30.0; pronotum ♂ 5.0, ♀ 6.4-6.5; tegmen ♂ 3.6, ♀ 5.9-6.1; hind femur ♂ 13.4, ♀ 14.7-17.2 mm. (Measurements based on material studied by the author.)

Type ♀. Type locality: Charles Is. Type lost.

Geographical distribution: Known only from Charles Is.

*Halmenus eschatus* Hebard, 1920

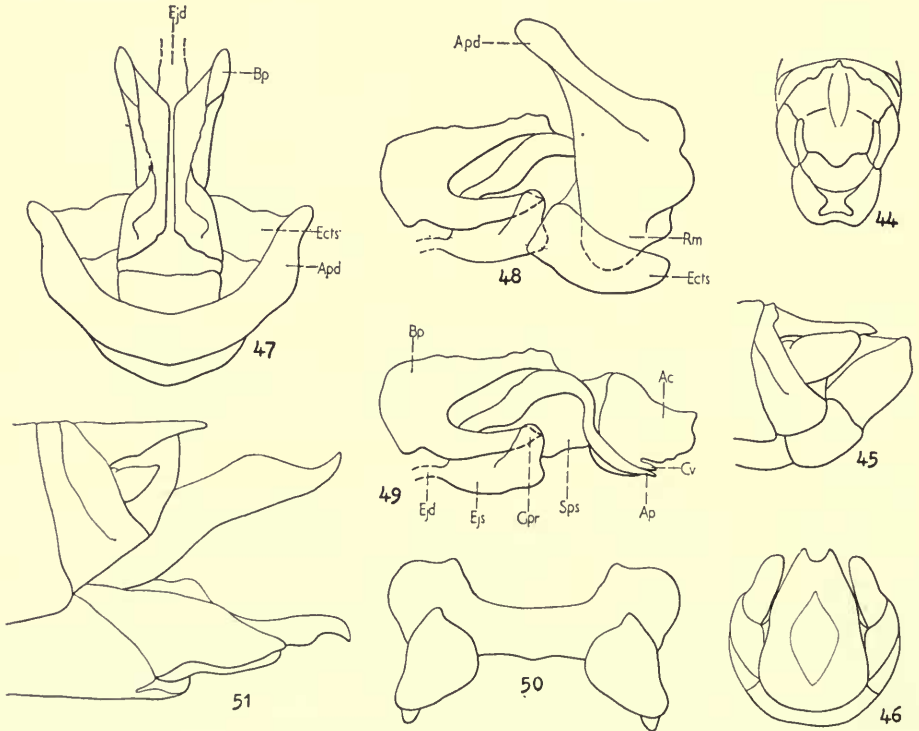
(Pl. 3, Text-figs. 44-51)

This is the most divergent species of the genus. Characters additional to those mentioned in the key are: tegmina in both sexes micropterous, being fully lateral and more strongly reduced than in other species; and interocular space much wider than in others.

Measurements: length: ♂ 20.8-23.5, ♀ 27.0-32.8; pronotum ♂ 5.2-5.9, ♀ 7.0-7.9; tegmen ♂ 3.5-4.0, ♀ 5.0-6.2; hind femur ♂ 10.4-11.3, ♀ 13.2-14.5 mm.

Type ♀. Type locality: 'Wenman Is.' Museum of California, Academy of Sciences. (Type No. 717.)

Geographical distribution: Known from type locality only.



FIGS. 44-51. *Halmenus eschatus*. Paratypes. 44, end of abdomen from above; 45, the same, lateral view; 46, the same, posterior view, to show excision of apex of subgenital plate; 47, phallic complex from above (epiphallus and most of ectophallic membrane removed); 48, the same, lateral view; 49, endophallus; 50, epiphallus; 51, ♀, end of abdomen, lateral view.

*Desmopleura concinna* Scudder, 1893

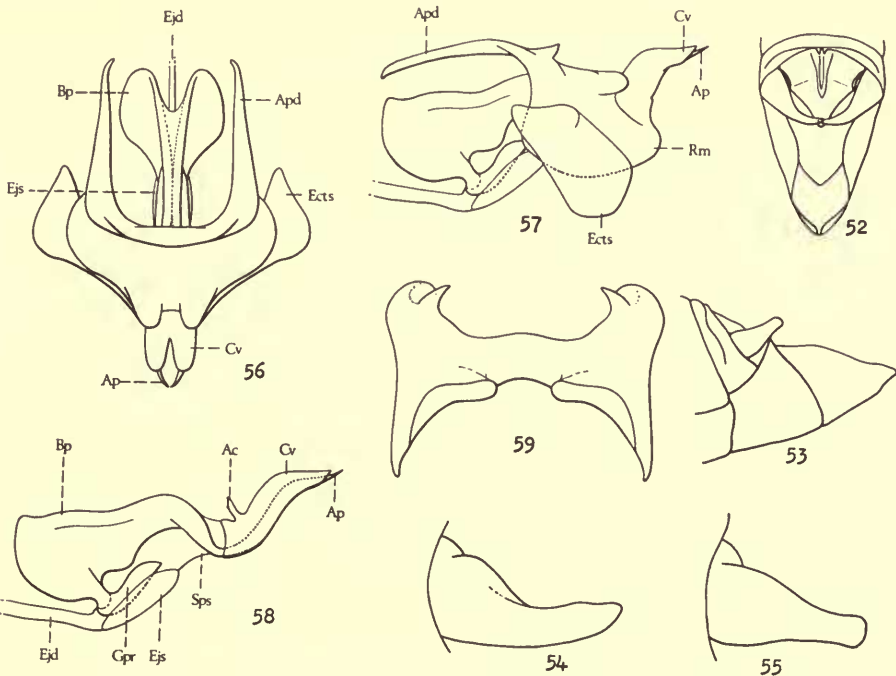
(Pl. 4, Text-figs. 52-59)

This genus belongs to subfamily Catantopinae of Acrididae, and probably to the group Podismini judging from the structure of the phallic complex.

No genus examined from the American continent is closely allied to *Desmopleura*. It may perhaps be related to the genus *Dichroplus*, but if so the relationship is rather remote.

Since only the male type is known, there is no possibility of studying it in detail and further material is needed.

♂ (Type. Redescription). Small. Integument slightly pitted. Antenna filiform, slightly shorter than head and pronotum together. Head obtuse, conical. Fastigium of vertex short obtuse-angular, sloping forwards, in middle with deep sulcus bordered by a pair of high, strong lateral carinulae which extend beyond base of vertex; linear median carinula running from middle of fastigium along whole head; frons oblique, frontal ridge narrow, sulcate, lateral carinulae obtuse. Pronotum subcylindrical, dorsum flattened, crossed by 4 fine sulci; median carina linear, crossed by posterior and preposterior sulci; lateral carinae absent; anterior margin straight, posterior broadly obtuse-angular; lateral lobe longer than high, margin excurved in middle, transverse sulci deep and comparatively wide. Prosternal process tongue-shaped, inclined backwards and touching mesosternum. Mesosternal interspace longer than wide;



FIGS. 52-59. *Desmopleura concinna*. Type. 52, end of abdomen, from above; 53, the same, lateral view; 54, cercus, from above; 55, the same, lateral view; 56, phallic complex from above (epiphallus and most of ectophallic membrane removed); 57, the same, lateral view; 58, endophallus; 59, epiphallus.

lateral lobe longer than wide, with rounded angle. Metasternal interspace elongate, closed. Tegmina and wings fully developed. Tegmen exceeding end of hind femur, rather narrow, reticulation sparse. Wing comparatively narrow, as long as tegmen. Tympanum well developed, large. Anterior and middle femora slightly inflated. Hind femur short and moderately slender. Lower basal lobe of hind knee rounded. External apical spine of hind tibia absent. Arolium large. Last abdominal tergite with a pair of small, narrow projections in middle. Supra-anal plate short, angular, at apex obtuse. Cercus wide in basal part, narrowing towards apex, which is strongly incurved; apex obtuse. Subgenital plate in profile elongate, narrow conical.

Phallic complex: Similar to that of the group Podismini: apical valve and valve of cingulum of penis covered by sheath; apical valves long, slender, at apices acute; valves of cingulum in profile slender, above fused, shorter than apical valves of penis; basal valves of penis large, strongly expanded; zygoma very large; apodemes slender, forming U-shaped structure. Epiphallus wide-bridged; ancorae small, acute, inclined inwards; lophi long and narrow, forming narrow lobes.

General coloration buff; from posterior margin of eye and extending along upper part of lateral lobe of pronotum, a wide blackish stripe; from apex of fastigium of vertex to posterior margin of pronotum, a dark brown stripe; carinula on head and median carina of pronotum lighter coloured than stripe; veins and veinlets of tegmen and wing brownish, membrane colorless. (Other parts of type specimen discolored due to previous preservation in fluid.)

Measurements: Length: 13.5, pronotum 3.2; tegmen 11.0; hind femur 9.0 mm.

Type ♂. Type locality: 'James Island'. United States National Museum, Washington.

### *Closteridia bauri* Scudder, 1893

(Pl. 5, Text-figs. 60-66)

♂. Of medium size, robust. Integument strongly rugose and granulose. Antenna filiform, longer than head and pronotum together, 20-segmented. Head subconical; fastigium of vertex acute-angular, as long as wide, lateral margins raised, median carinula well developed, fastigial foveolae narrow-rhomboidal, deep, with prominent edges; frons inclined backwards, frontal ridge narrow, sulcate, lateral carinulae high, almost parallel, slightly diverging basally; facial carinulae high, slightly incurved; weak occipital carinula present. Pronotum subcylindrical, widened backwards, dorsum indistinctly separated from lateral lobes; median carina irregularly linear, in prozona slightly raised; lateral carinulae lyrate, limiting narrow elevation of dorsum; transverse sulci indistinct; posterior margin of metazona corrugated; posterior angle of lateral lobe roundly protruding backwards. Prosternal process absent. Mesosternal interspace twice as wide as long. Metasternal interspace wider than long. Tegmina vestigial; wings and tympanum absent. Metanotum and first abdominal tergite with rough median carinula. Hind femur short, stout, reaching end of abdomen. Lobes of hind knee with apices rounded. Hind tibia slightly shorter than femur; external apical spine absent; spurs short, of equal length; arolium slightly longer than half length of claws. Last abdominal tergite slightly and regularly incurved. Supra-anal plate slightly longer than wide, angular, at apex obtuse, slightly incurved, in basal part with small median concavity, transverse ridge in middle well developed. Cercus short, conical. Subgenital plate short, subconical.

Phallic complex: of Acridinae type. Apical valve of penis short, much shorter than valves of cingulum; basal valves large and strongly expanded; apodemes relatively small, forming wide, arch-like structure. Epiphallus robust, ancorae large, inclined inwards; lophi very large, irregularly bilobate.

General coloration rust-brown, mottled with dark brown spots; head above and dorsum of pronotum lighter, dirty ochraceous; outer and inner sides of hind femur with two transverse, brown fasciae; hind tibia dirty ochraceous.

♀ (Type). See original description.

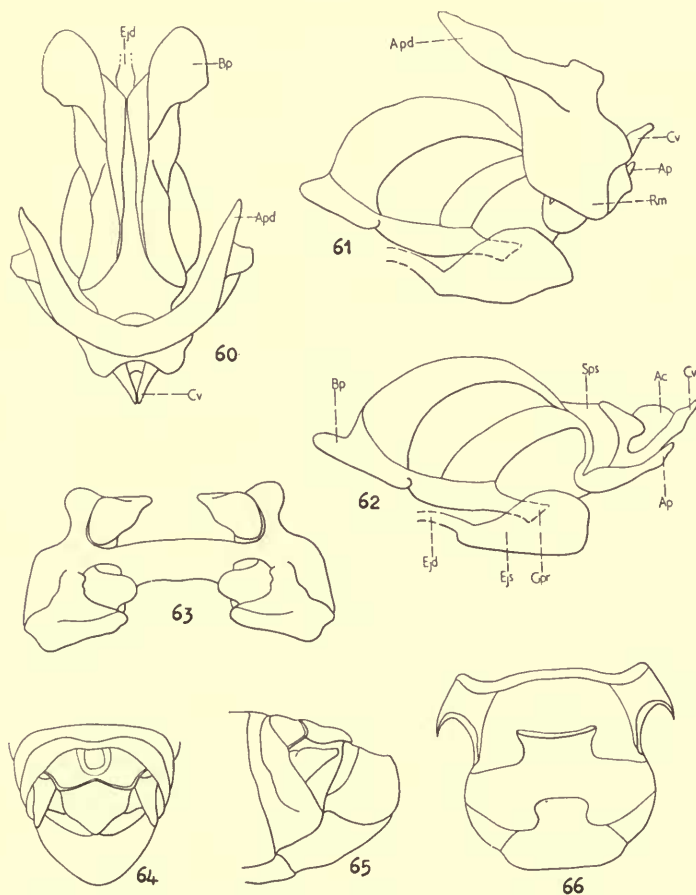
Length: ♂ 20.0, ♀ 22.0; pronotum ♂ 4.3, ♀ 4.5; tegmen ♂ 0.3, ♀ absent (?); hind femur ♂ 11.0, ♀ 13.5 mm.

Type ♀ (lost). Type locality 'Wreck Bay, Chatham Is.'

♂. Described by Hebard (1920) and redescribed above. Cowley Mountain, Albemarle Is. Museum of the California Academy of Sciences.

Only two specimens of this remarkable genus and species are known; and since the female type is lost, it is not possible to verify that both specimens belong to the same species. They are practically wingless and were collected on different and widely separated islands.

This genus is of the subfamily Acridinae of Acrididae (*sensu* Dirsh, 1961). No close relatives of it are known from America and its phylogenetic relationship is obscure.



FIGS. 60-66. *Closteridia bauri*. 60, phallic complex from above (epiphallus and most of ectophallic membrane removed); 61, the same, lateral view; 62, endophallus; 63, epiphallus; 64, end of abdomen, from above; 65, the same, lateral view; 66, meso- and metasternum.

*SPHINGONOTUS* Fieber, 1852

It was rather surprising to find the genus *Sphingonotus* represented on the remote Galapagos Islands. This presents a puzzling zoogeographical problem, even though *Sphingonotus* is the most widely distributed genus of all Acridoidea. It occurs over the whole of Europe, Africa, most of Asia (including Japan), Australia, Jamaica, Ecuador and the Galapagos Islands.

The most numerous specific complex of the genus occurs in Central and South-west Asia and in the palaeartic part of Africa.

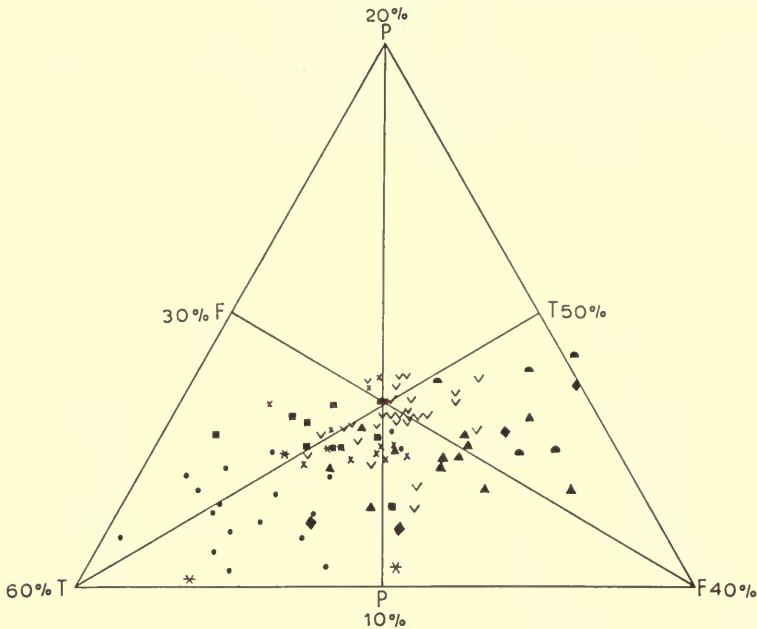
It is a peculiar fact that the species from Galapagos (Text-figs. 67-70), Jamaica (Text-figs. 71-74), and the type-species *S. caerulans* (Text-figs. 75-79) from Sweden have remarkably similar phallic complexes. (The one known specimen from Ecuador, actually from Puna Island, is a female, but externally it is very similar to the species from Galapagos.)

This indicates a relatively recent separation of these species and a relatively recent penetration by them to America and the Galapagos Islands. We have no indication of how this occurred. The distances between the Palaeartic Region, Jamaica, Ecuador and Galapagos are enormous, and *Sphingonotus* has not so far been found in intervening countries. At present it is only possible to affirm a close affinity between the species on the basis of morphological characters, leaving zoogeographical considerations until more data become available.

Stål in 1860 described *Oedipoda fuscoirrorata* (at present *Sphingonotus fuscoirroratus*) from two females from 'Galapagos' and one female from Puna Island, about two miles from the coast of Ecuador. Snodgrass (1902), who considered the specimen from Puna Island different from the Galapagos specimens, restricted the name *fuscoirrorata* Stål to the specimen from Puna Island and gave new names, *trinesiotis* and *tetranesiotis*, to two alleged species from Galapagos, which include Stål's specimens, on the grounds that Stål did not fix the type locality. Here Snodgrass' action is considered incorrect and not valid, on the grounds that Stål had two females from Galapagos and one female from Puna Island and in his original description mentioned their localities as 'Galapagos Is. and Puna Is.', not vice versa as stated by Snodgrass. For this reason Stål's name *Oedipoda fuscoirrorata* Stål, 1860 is accepted here as the original name for the Galapagos species, but for the specimen from Puna Island the specific name ***punensis* nom. n.** is proposed.

In the same paper Snodgrass (1902), who assigned *trinesiotis* and *tetranesiotus* to *Sphingonotus*, described three subspecies of the former and four of the latter. Hebard (1920) synonymized all of them, including the specimen from Puna Island, under Stål's original name *fuscoirrorata*. In the light of the present study Hebard's synonymy is correct, except for the specimen from Puna Island whose position is doubtful as only one specimen is known. From the present author's point of view it seems preferable to retain the specimen from Puna Island as a separate species of *Sphingonotus*. By all external characters, this specimen is very similar to the Galapagos species, except that the metazona of the pronotum (Pl. 7) is relatively shorter and its posterior margin is widely obtuse-angular, almost rounded, while in the Galapagos species it is acute-angular, and obtuse only at the apex (Pl. 6).

A study of the series of the species and subspecies of Snodgrass from the topotypical localities shows that they cannot be separated by external morphological characters or by the phallic complex. When studied morphometrically they display some tendency towards forming races on the different islands. When three morphometric characters (length of pronotum—*P*, length of tegmen—*T* and length of hind femur—*F*) are studied and plotted as triangular co-ordinates (Graph 2) these various forms show such a tendency, but they overlap so widely that to consider them as races would be stretching the point too far. Probably, in spite of being small and not such good fliers as *Schistocerca*, they can still fly from island to island, levelling the morphological and morphometric features of the population.



GRAPH 2. Triangular co-ordinates showing distribution of proportional values of length of pronotum (*P*), length of tegmen (*T*) and length of hind femur (*F*), expressed as percentages. ●—Hood Is., ▲—Indefatigable Is., ■—Charles Is., ×—Narborough Is., V—Albemarle Is., \*—Chatham Is., ◆—Abingdon Is., ▲—James I.

### *Sphingonotus fuscoirroratus* (Stål, 1860)

(Pl. 6, Text-figs. 67–70)

*Oedipoda fuscoirrorata* Stål, 1860 : 345 (partim). LECTOTYPE ♀ 'Galapagos Is.' by present selection. Stockholm Museum.

*Sphingonotus trinesiotis* Snodgrass, 1902 (Hebard, 1920 : 321).

*Sphingonotus trinesiotis chathamensis* Snodgrass, 1902 : 437 (Hebard, 1920 : 321). Type ♂, lost.

*Sphingonotus trinesiotis indefatigabilensis* Snodgrass, 1902 : 437 (Hebard, 1920 : 321). Type ♂, lost.

*Sphingonotus trinesiotis albemarlensis* Snodgrass, 1902 : 437 (Hebard, 1920 : 321). Type ♂, lost.

*Sphingonotus tetranesiotis* Snodgrass, 1902 : 437 (Hebard, 1920 : 321).

*Sphingonotus tetranesiotis charlesensis* Snodgrass, 1902 : 437 (Hebard, 1920 : 321). Type ♂, lost.

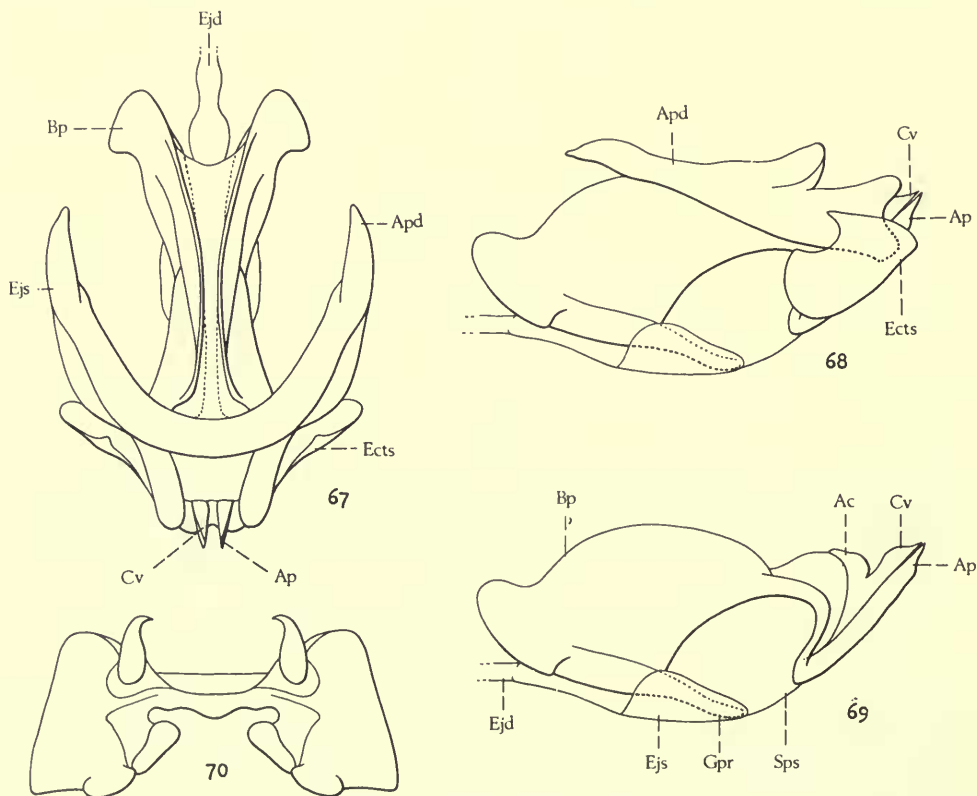
*Sphingonotus tetranesiotis barringtonensis* Snodgrass, 1902 : 437 (Hebard, 1920 : 321). Type ♂, lost.

*Sphingonotus tetranesiotis hoodensis* Snodgrass, 1902 : 438 (Hebard, 1920 : 321). Type ♂, lost.

*Sphingonotus tetranesiotis indefatigabilensis* Snodgrass, 1902 : 438 (Hebard, 1920 : 321). Type ♂, lost.

The female specimen of *Oedipoda fuscoirrorata* Stål, 1860 which was quoted in Sjöstedt's 1932 paper as the type is selected here and described below as lectotype. All three of Stål's original specimens were studied.

Redescription. ♀ Lectotype. Integument rugose and granulose. Antenna shorter than head and pronotum together. Fastigium of vertex sloping forwards, concave and widening in front; lateral and median carinulae well developed; frontal ridge slightly widening at ocellus, constricted below ocellus and undulating below. Pronotum rugose and granulose, dorsum crossed by 3 sulci; median carina slightly elevated in front of anterior sulcus, obliterated between



FIGS. 67-70. *Sphingonotus fuscoirroratus*, from Charles Is. 67, phallic complex, from above (epiphallus and most of ectophallic membrane removed); 68, the same, lateral view; 69, endophallus; 70, epiphallus.



anterior and posterior sulci and sharply linear in metazona; in front of posterior sulcus a concavity with a pair of small elevations posteriorly; metazona about half as long again as prozona, its posterior end acute-angular, apex obtuse, sides undulated; anterior angle of lateral lobe of pronotum obtuse-angular, posterior angle with acute-angular projection. Tegmina exceeding end of abdomen; intercalary vein of medial area almost parallel to medial vein. Mesosternal interspace short, twice as wide as long. Subgenital plate at apex truncate. Ovipositor short, valves curved at apices; lower valve with angular, lateral, external projection.

General coloration brownish; tegmen with 2 dark brown transverse fasciae and with small spots in apical part; wings hyaline, slightly infumate.

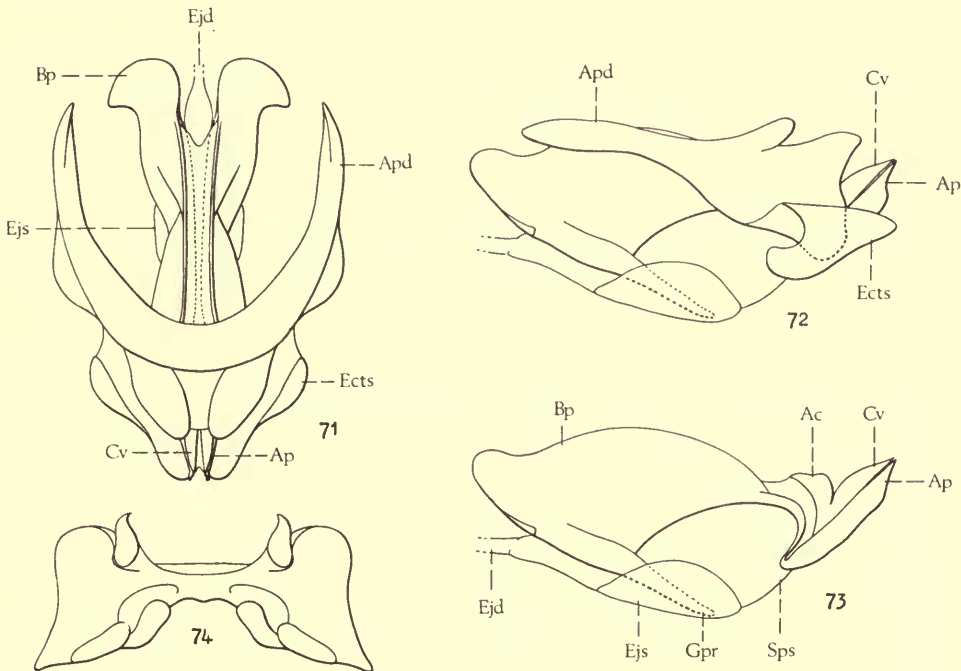
♂. Much smaller than female. Antenna longer than head and pronotum together. Fastigium of vertex more sloping forwards, narrower, more concave. Last abdominal tergite with a pair of small, rounded projections; supra-anal plate short, angular. Cercus narrow-conical, at apex obtuse. Subgenital plate short, obtusely subconical.

Phallic complex of usual type for the genus (see Text-figs. 67-70).

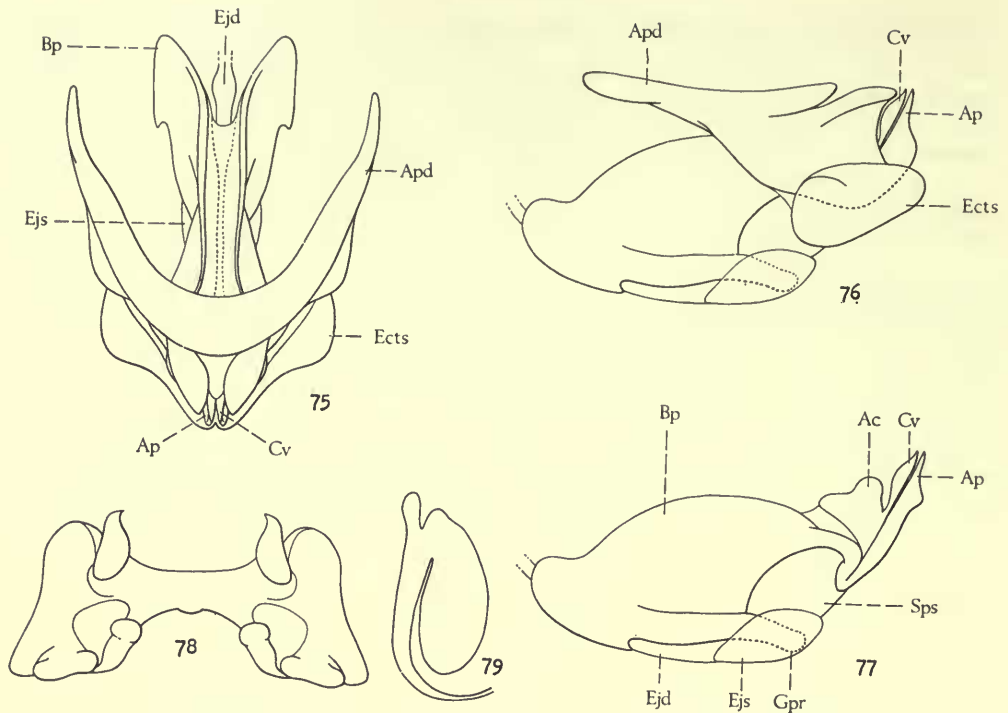
General coloration as in female; wing more infumate.

### Measurements (mm.)

		Length of body	Length of pronotum	Length of tegmen	Length of hind femur
♂	Range	10.9-17.7	2.3-3.5	9.3-14.8	6.4-10.2
	Average	13.8	2.9	12.6	7.9
♀	Range	16.1-24.0	3.2-4.6	13.8-21.2	8.4-12.9
	Average	20.8	4.0	17.3	10.7



FIGS. 71-74. *Sphingonotus jamaicensis* (Saussure, 1884). 71, phallic complex, from above (epiphallus and most of ectophallic membrane removed); 72, the same, lateral view; 73, endophallus; 74, epiphallus.



FIGS. 75-79. *Sphingonotus caeruleus* (Linnaeus, 1767). 75, Phallic complex from above (epiphallus and most of ectophallic membrane removed); 76, the same, lateral view; 77, endophallus; 78, epiphallus; 79, spermatheca.

Lectotype ♀. Lectotype locality 'Galapagos Is.' Stockholm Museum.

Geographical distribution: Abingdon, Albemarle, Barrington, Charles, Chatham, Gardner (near Hood), Hood, Indefatigable, James, Jervis, Narborough, Seymour (both).

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